

LABORATORY STUDIES OF THE FACTORS STIMULATING BALLOONING BEHAVIOR BY LINYPHIID SPIDERS (ARANEAE, LINYPHIIDAE)

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ABSTRACT. Linyphiid spiders were tested individually in the laboratory in order to assess possible factors stimulating the onset of ballooning behavior. An air flow chamber was used for many of the tests. Air movement was found to be an important stimulus for initiating both the climb to a prominent position and subsequent take-off attempts. After instigation of pre-flight behavior by an initial air flow stimulus, climbing continued in still air, though take-off attempts generally ceased in the absence of further air movement. Neither circadian rhythmicity nor darkness were found to prevent exhibition of ballooning behavior at night. Length of time spent attempting to take-off appeared to be a factor in reducing a spider's response to the stimuli causing ballooning behavior.

Ballooning is the term commonly used to describe aeronautic dispersal using wind drag on threads of silk for lift, as exhibited by several families of spiders. At certain times of the year these spiders take to the air en masse, though there are lower numbers ballooning throughout the year (Freeman 1946; Sunderland 1991; Weyman et al. 1995). There must be innate factors governing which spiders will balloon and at what stage during their lifetime, possibly with environmental factors adjusting the likelihood of its occurrence at a particular time (see Weyman 1993 for a review). However, occurrence of this critical component of spider population dynamics is finally driven by individual behavior in response to immediate stimuli.

Although several studies have been carried out to investigate when, and under what meteorological conditions, spiders take to the air (e.g., Greenstone 1990; Vugts & van Wingerden 1976; Thomas 1993), very little work has been done on the immediate factors that stimulate spiders to initiate and cease the behaviors that result in flight. The current investigation explored some of the factors that may be responsible by observing individual spiders subjected to a variety of stimuli in the laboratory. This set of basic experiments assessed the importance of each stimulus, to detect those which are worthy of more intensive investigation.

Air flow is an important factor in ballooning because it provides the source of power for spider

flight (Humphrey 1987; Suter 1991, 1992). It would seem likely, therefore, that air movement might be the stimulus that elicits ballooning behavior (taken here to include the pre-flight behaviors). It is well documented that spiders will not take off in wind speeds over 3 m/s (Richter 1970; van Wingerden & Vugts 1974; Vugts & van Wingerden 1976; Greenstone 1990). There is also limited evidence that spiders do not balloon at night (Bishop 1990). Suction trap data (Sunderland unpubl.) show extremely low numbers of spiders caught at night, even between high day catches (maximum night catch of 5, compared with a maximum day catch of 178). There are two possible explanations for this: 1) that meteorological conditions at night are not suitable for ballooning; 2) that pre-flight behavior (climbing to a high point and attempting to take-off) ceases at a certain time in response to the light-dark cycle or an endogenous circadian rhythm.

Laboratory experiments were carried out in an air flow chamber, similar to one used by Legel & van Wingerden (1980), to determine whether air movement was a sufficient stimulus to elicit climbing and take-off behavior. Further experiments were carried out to determine whether climbing and take-off behavior require continuous stimuli, or whether they continue after a short initial stimulus, in the manner of a fixed action pattern (FAP) (Manning 1979).

The hypothesis that ballooning does not occur

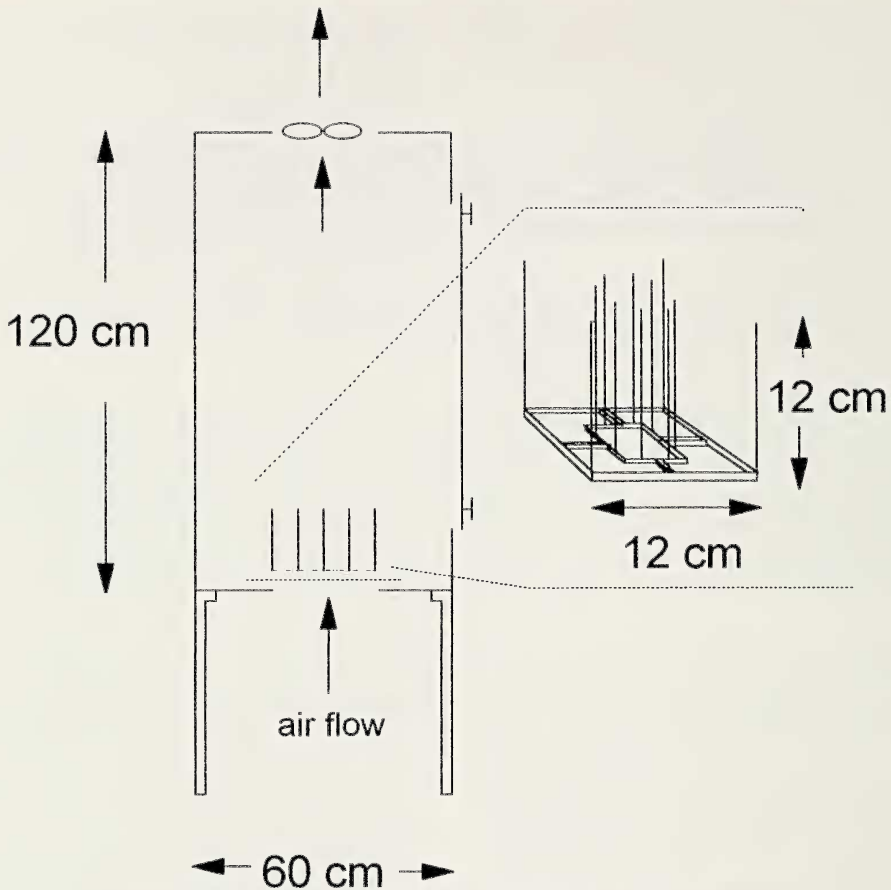


Figure 1.—Schematic diagram of the laboratory air flow chamber.

at night for behavioral reasons was tested in the laboratory. Evidence for an endogenous circadian rhythm was sought by subjecting spiders to ballooning stimuli during the night. Other spiders were tested for ballooning behavior in effective darkness. Duration of the ballooning behavior was also assessed as a possible factor limiting a spider's responsiveness to the stimuli presented.

METHODS

Collection of spiders.—*Erigone* spp. were collected as required from unsprayed grassland on a farm 20 miles north of Southampton, UK, by Dietrick vacuum insect net (D-vac). Samples were sorted on the day of collection and spiders were placed individually in 3 cm diameter Petri dishes with a small piece of moistened filter paper to avoid desiccation. *Erigone* spp. were identified live under a binocular microscope before testing,

or preserved in 70% alcohol after testing awaiting identification. The spiders were not identified to species, but only *E. atra* (Wid.) and *E. dentipalpis* (Bl.) were found at the collection site in population samples during 1991 and 1992. These two species are expected to exhibit very similar behaviors as they have virtually identical life-cycles, niches and habits (De Keer & Maelfait 1988). Storage and testing of spiders were carried out in a controlled environment room at $18^{\circ}\text{C} \pm 2$, relative humidity $70\% \pm 10$, L16:D8 cycle (approximately in phase with external conditions), except where stated otherwise.

The air flow chamber.—The laboratory air flow chamber used here was an acrylic sheeting ("perplex" or "Plexiglas") box 120 cm high, with a 55×60 cm base (Fig. 1). A suction fan in the top (Rotron Inc. Whisper Fan WR3A1, 230V AC, 12W) drew air through a 12×12 cm square opening in the center of the base, covered with metal gauze as a support. White netting covered

the whole of the base to aid viewing and a wooden climbing frame with 12 cm uprights was placed over the opening. The updraft at 1 cm above base level in the frame was $0.57 \text{ ms}^{-1} \pm 0.01$ (measured with a Solomat MPM 500e hotwire anemometer, 950 readings logged at 5 s intervals). Take-off within the confines of the chamber was not normally possible but pre-flight behavior could be observed and recorded easily. This chamber was also used by Weyman et al. (1994, 1995).

Erigone spp. are ground-dwelling spiders which do not normally climb (C. J. Topping pers. comm.), except when motivated to balloon. Having climbed to a prominent position, prior to take-off, a spider assumes the position known as "tip-toe" (Richter 1970), with legs extended and abdomen raised, and releases silk until the drag on the length of silk is sufficient to lift the spider from the substrate, or possibly until some higher optimal threshold is reached. In an alternative take-off behavior, referred to here as "dropping" (after Jones 1994), the spider drops a short way on a thread, while a second thread provides wind-drag for lift.

Factors eliciting ballooning behavior.—*Air flow as the stimulus for climbing in the laboratory:* The individual Petri dishes containing spiders were maintained in a large plastic container with high r.h. ($\approx 100\%$) achieved by putting a small amount of water in the base. Testing for climbing behavior was then carried out in the laboratory air flow chamber. To observe the effect of airflow on the behavior of spiders previously in calm conditions, individual spiders were first observed in still conditions, then with air movement over them. Individual Petri dishes containing spiders were placed in the center of the climbing frame, with the fan off. A piece of plasticine ("modeling clay") was attached to the lid of the Petri dish, attached to a cotton thread running out through a hole in the top of the chamber. The door of the chamber was then closed and the lid gently lifted off the Petri dish by pulling the cotton thread. The spider was observed for three minutes before the fan was switched on. Observations then continued for a further three minutes. Wind speed just above the open Petri dish was found to be 0.0 m/s with the fan off, and fluctuated between 0.0–0.1 m/s with the fan switched on (measured with a Solomat MPM500e hotwire anemometer). Three separate experiments were carried out, with groups of 10, 29, and 29 spiders respectively.

Air flow as the stimulus for take-off behavior in the laboratory: To determine the necessity of continuous air flow as a stimulus for ballooning behavior, 16 spiders were individually subjected to a short stimulation/disturbance by collection in a hand aspirator, and placed into the climbing frame in the chamber with the fan off. Each spider was observed for three minutes. Climbing and "tip-toe" behaviors were recorded. After a short rest period the same spiders were re-tested in the same way, but with the fan turned on.

To further examine the effect of changing air flow stimulus, individual spiders were placed into the climbing frame, with the fan off, and observed for 44 minutes with the fan alternately turned on or off at ten minute intervals, starting with a still period. The occurrence of several behavioral categories was recorded: moving or stationary at base level (assigned the term "ground"); climbing the uprights ("climbing"); activity at the top of the uprights ("top active"); inactivity whilst at the top of the uprights ("top inactive"); take-off attempts by the dropping method ("dropping"); take-off attempts by the tip-toe method ("tip-toe"). The experimental time was divided into 30 s periods, and assessment of behavior was by a standard presence or absence (1/0) method during each 30 s. The most advanced behavior towards take-off was noted for each 30 seconds. This method gave four interfaces of changing conditions for each spider tested and would show any possible effects of previous conditions on subsequent ballooning behavior. Ten minute intervals were used to allow valid assessment of individual behavior types over a large number of 30 s periods between each interface, with the final four minutes to allow any change after the final interface to become clearly apparent. Sample intervals of 30 s were chosen by experience, for logistic reasons. Four individuals were tested in this way, each constituting an independent repetition.

Factors limiting response to initiation stimuli.—*Testing for endogenous rhythms:* Testing was carried out in a portable ballooning chamber, similar to the one described above but modified with a plywood base and a DC fan (Papst multifan 4132, 9 cm, 12 V DC, 5W), giving an equivalent air flow. The chamber was situated in a room which did not have environmental control facilities, but variations in ambient humidity and temperature over the experimental period were not expected to affect the results. The room was illuminated naturally during the day and by a

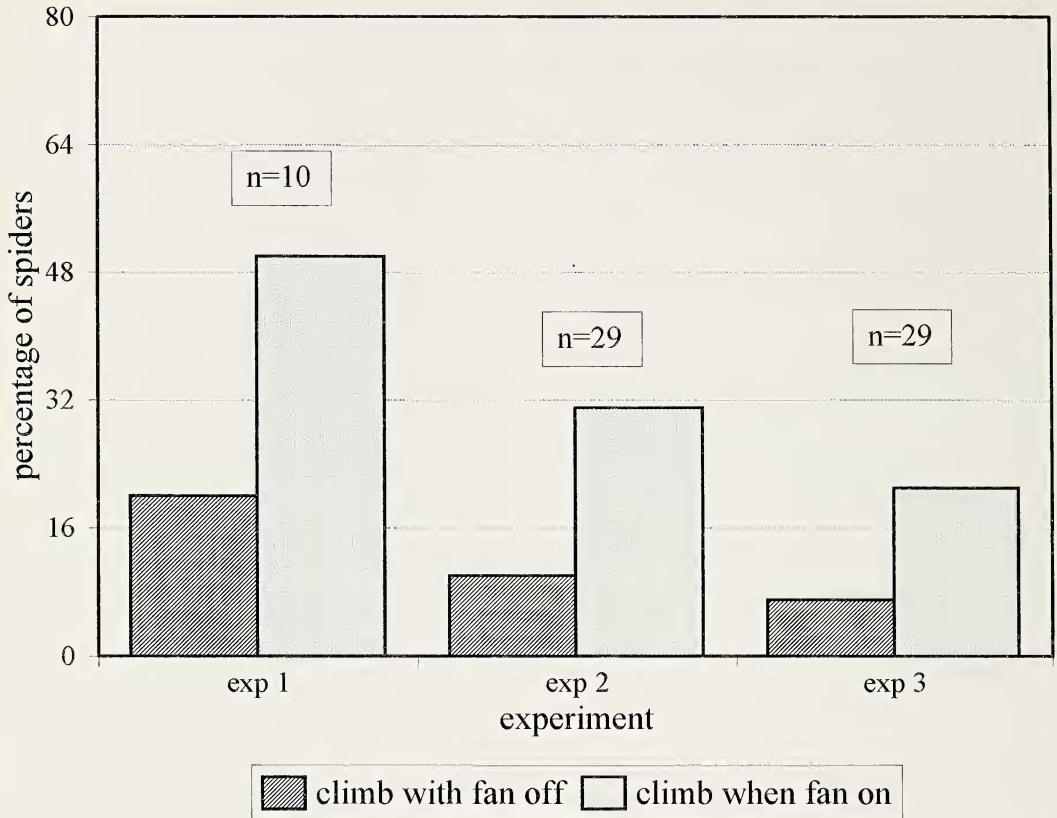


Figure 2.—The percentage of spiders climbing during the test period with the fan off, and the additional number climbing after the fan was switched on.

100 W incandescent source during dark hours only while testing was in progress. The results gained could be used to assess the necessity for more controlled conditions.

Thirty-two spiders were individually tested for pre-aeronautic behavior within three minutes of being placed via hand aspirator onto the base of the wooden frame. Climbing and “tip-toe” behaviors were recorded over a three minute period. The spiders were tested once during the daytime, once during darkness, and once again in the following light period. This was repeated for each spider on the subsequent day.

Testing for limitation of ballooning response in darkness: To test whether darkness limits response by spiders to a ballooning stimulus, linyphiids were collected by hand aspirator as they attempted to take-off from fences and grass at the field collection site. The spiders were placed individually in Petri dishes then placed into an opaque box. The spiders were kept in the box for approximately three weeks before being assessed for ballooning behavior.

Testing was carried out in an open arena with a fan blowing across it, where infra-red lighting was available, and where take-off was possible. Spiders are not thought to be sensitive to infra-red light (M. F. Land pers. comm.). Light intensity at floor level, where the spiders were placed, was 0.05μ Einsteins/m²/s (readings taken with a Li-Cor model Li-185B photometer). Ten spiders from the opaque box were individually tested for three minutes. Climbing, “tip-toe”, and take-off behaviors were recorded.

Testing for limits to duration of time spent attempting take-off: To assess the duration of ballooning behavior, individual spiders were initially given six min in the laboratory ballooning chamber, with the fan on, to initiate ballooning behavior. Presence or absence of “ground”, climbing, “dropping” and “tip-toe” behaviors was determined over one min periods. If a spider exhibited ballooning behavior then it was allowed to continue until it descended to ground level and remained there for six consecutive min, with no indication of further climbing. The test

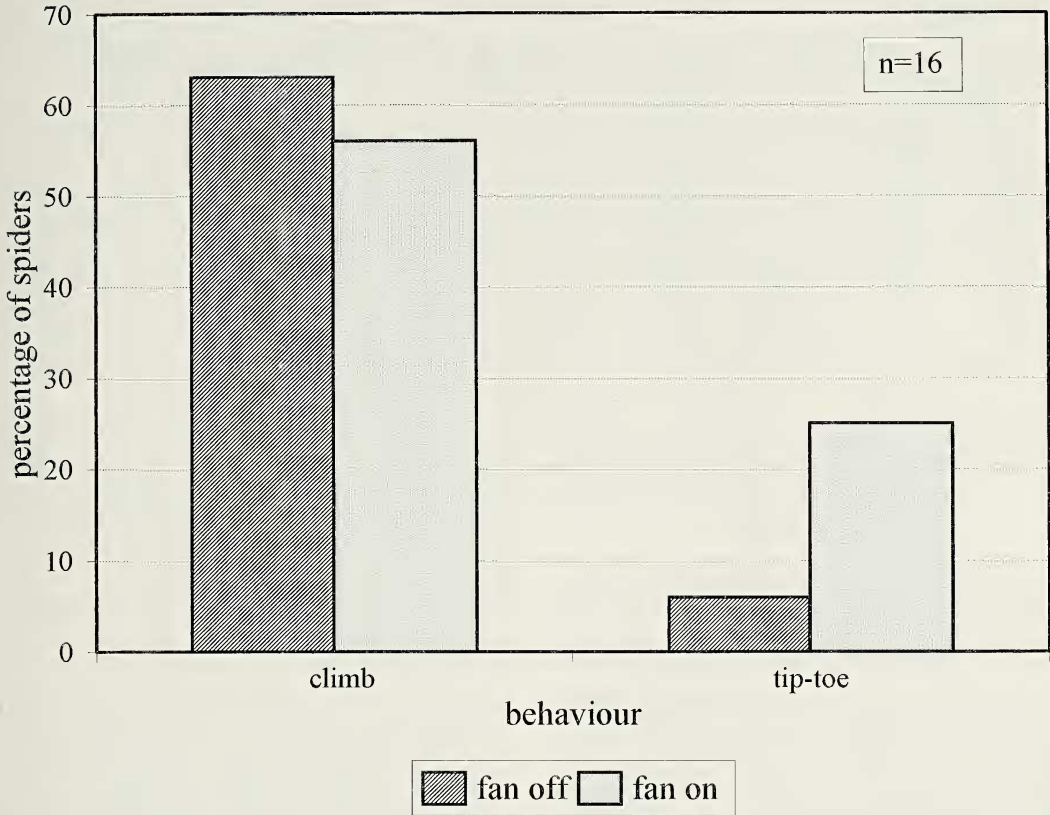


Figure 3.—The behaviors exhibited in the ballooning chamber within three minutes of release with the fan either on or off, after the initial stimulation by hand aspiration.

was then terminated. Individuals were re-tested to determine whether cessation was permanent or temporary. Six min was allowed to give added assurance of a spiders intent to start or stop ballooning, compared to the usual three min period of other experiments. This was important because the experiment was designed to measure accurately time spent showing ballooning behavior for individual spiders, rather than being a qualitative comparison between different groups or conditions, as made in experiments with the shorter time period. A total of 45 tests was carried out on 21 spiders.

RESULTS

Factors eliciting ballooning behavior.—*Air flow as the stimulus for climbing:* A small proportion of spiders climbed with the chamber fan switched off. They may have responded to air movement lower than the threshold of the measuring equipment, or to disturbance as the Petri dish lid was

removed (Fig. 2). The onset of air flow elicited climbing for most of the spiders, however.

Air flow as the stimulus for take-off behavior: After aspiration, as many of the 16 spiders climbed with the fan off as when it was on (Fig. 3), with no significant difference between the tests ($G = 0.1$, $df = 1$, $P > 0.05$). Although climbing behavior often ensued following the initial stimulus, “tip-toe” behavior was rare and only increased after further stimulation (Fig. 3), though the observed difference was not significant ($G = 2.3$, $df = 1$, $P > 0.05$). The limitations of the G -test in this context, where repeated measures are made on the same subjects, are recognized. It is used here as a simple indicator of the level of differences between tests.

In the second set of experiments, where four spiders were tested individually for 44 min each, pre-flight climbing again continued in the absence of the air stimulus (Figs. 4–7). This may suggest the existence of a FAP for ballooning behavior. “Tip-toe” behavior was again largely

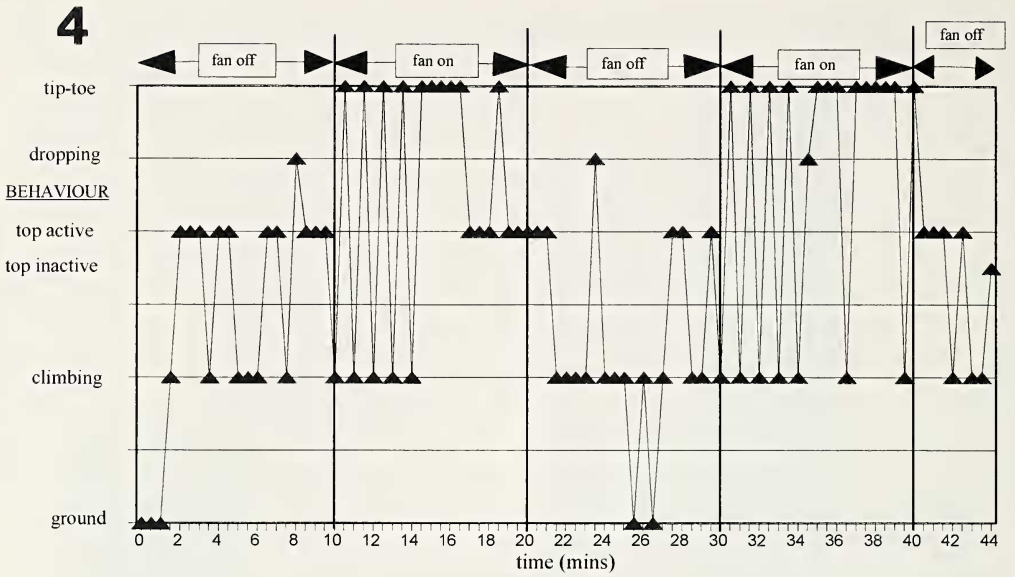


Figure 4.—The effect of air movement on pre-ballooning behavior for spider A. Behavior recorded in 30 second periods with fan on or off.

dependent on air flow, but did occasionally appear to be exhibited in its absence. This was difficult to assess, however, because spiders did not seem to fully extend into the “tip-toe” position unless the silk thread released was being pulled by the updraft. All four spiders tested showed marked differences in their behavior when the fan was switched on or off. Most no-

ticeably, a much higher proportion of time was spent tip-toeing with the fan on, and more time was spent climbing with the fan off (Table 1). Only spider B showed signs of ending ballooning behavior during the 44 min period (Fig. 5).

Factors limiting response to initiation stimuli.—Endogenous rhythms: Spiders showed climbing and “tip-toe” behaviors at all test times

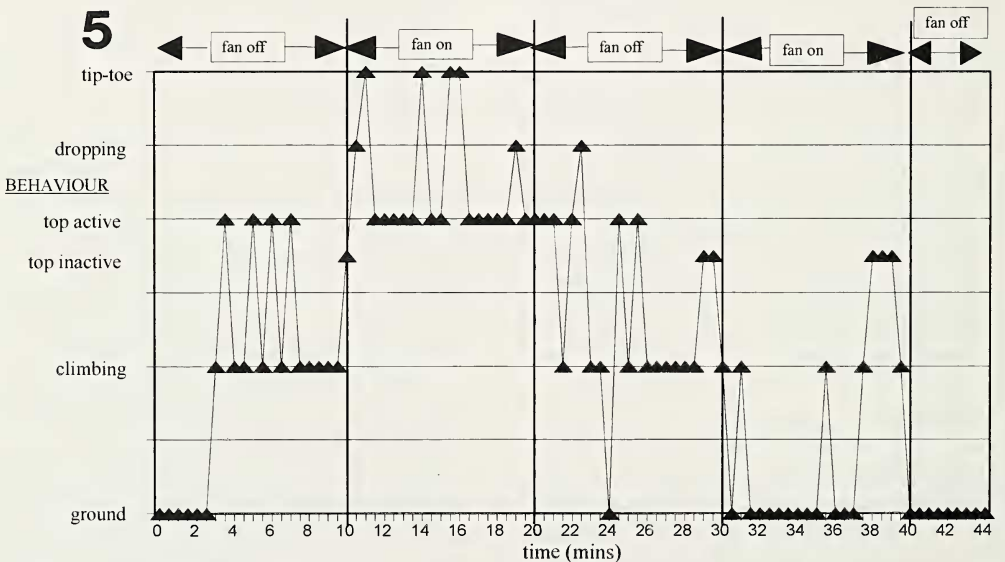


Figure 5.—The effect of air movement on pre-ballooning behavior for spider B. Behavior recorded in 30 second periods with fan on or off.

Table 1.—The proportion of the total assessment points at which each behavior was exhibited by each of four spiders.

Behavior	Spider A		Spider B		Spider C		Spider D	
	Fan on	Fan off	Fan on	Fan off	Fan on	Fan off	Fan on	Fan off
Tip-toe	0.575	0.000	0.100	0.000	0.500	0.083	0.550	0.021
Dropping	0.025	0.042	0.050	0.021	0.000	0.021	0.150	0.042
Top active	0.150	0.396	0.375	0.167	0.400	0.271	0.225	0.354
Top inactive	0.000	0.021	0.075	0.063	0.000	0.000	0.000	0.021
Climb	0.250	0.458	0.100	0.438	0.100	0.542	0.075	0.563
Ground	0.000	0.083	0.300	0.313	0.000	0.083	0.000	0.000
	40	48	40	48	40	48	40	48

(Table 2), with no significant differences between times (G -test, $P > 0.05$, $df = 2$), suggesting that there is no endogenous circadian rhythm limiting ballooning behavior at night. Statistical limitations of the G -test apply, as stated above.

Effect of darkness: Ten spiders were tested under infra-red light. Six of these showed ballooning behavior: three of the six showed climbing and "tip-toe" behavior, and three climbing and "dropping". One of the tip-toeing spiders became airborne.

Duration of time spent attempting to take-off: Of the 21 spiders tested, ten showed ballooning behavior on at least one occasion. A total of 16 ballooning periods was observed. Time to cessation of ballooning behavior ranged from 3–267 min. The mean duration \pm SD was 48 min \pm 73. Six of the 16 ballooning periods were in retests of spiders that had shown ballooning behavior on a previous occasion, suggesting that respites are only temporary. There was no in-

Table 2.—Percentages of spiders showing pre-ballooning behavior during the day and at night in the laboratory ballooning chamber. (ns = not significant) (dark at 1930 h).

Testing time	% climbing	% tip-toeing	Number tested
Replicate 1			
1800–1930 h	53%	44%	32
0000–0140 h	72%	44%	32
1100–1300 h	56%	32%	32
G -statistic	2.6 (ns)	1.4 (ns)	
Replicate 2			
1400–1600 h	63%	25%	32
2220–2400 h	63%	41%	32
0940–1140 h	48%	23%	31
G -statistic	1.8 (ns)	2.8 (ns)	

dication of individuals having set durations for ballooning behavior periods, one spider showing a range of 8–129 min to cessation.

DISCUSSION

Air flow was indicated as an important initial stimulus in the initiation of ballooning behavior. In the experiment to determine whether air flow is the stimulus for climbing it could be argued that the extra time allowed more spiders to exhibit climbing during the second three min period, with the fan on. However, many spiders were observed to have an immediate and strong climbing response as soon as the fan was turned on, indicating the importance of air flow as a stimulus.

When spiders were tested under infra-red lighting, to which they are thought to be insensitive, ballooning behavior could still be instigated. Thus darkness was not found to limit ballooning. Spiders tested for ballooning tendencies at different times showed no indication of an endogenous circadian rhythm limiting ballooning after dark. These results do not necessarily mean that spiders regularly balloon at night, but they certainly suggest that there is no endogenous reason why they should not, due to circadian rhythms or photo-responsiveness. Meteorology is implicated as the major factor limiting ballooning at night. Conditions may simply not be suitable for take-off, even if spiders are attempting to fly at night. Farrow (1982, 1986) found spiders flying in large numbers at night in the upper air. However, this was facilitated by a nocturnal temperature inversion which actually prevents take-off as the surface air cools. The spiders, therefore, took off during the daylight hours, and remained aloft until re-inversion of the temperature gradient the next day. Observations might reveal spiders attempting to take-off at

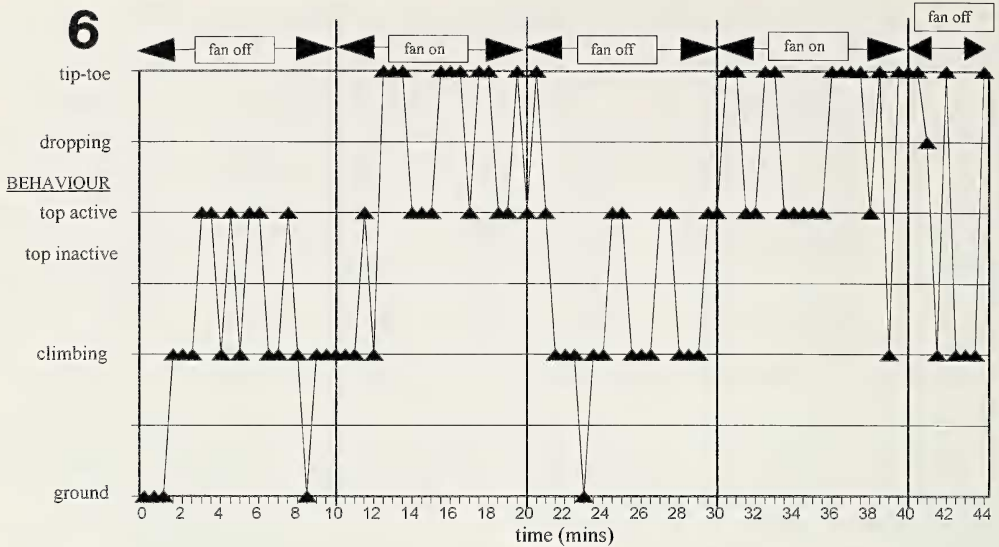


Figure 6.—The effect of air movement on pre-ballooning behavior for spider C. Behavior recorded in 30 second periods with fan on or off.

night in greater numbers than previously recorded, but not succeeding.

It appears that, once initiated, ballooning behavior is carried to completion (take-off, when possible) or until some limit is reached (indicated here as temporal or energetic), even if the stimulus is removed. This suggests that some sort of fixed action pattern (FAP) acts to maintain the behavior for some time after initiation, in the

absence of further stimulus. An alternative explanation could be that a lack of air movement provided the stimulus for continuation of the behavior when the fan was switched off. However, lift from an updraft is necessary for take-off so it would be expected that spiders should stop the pre-ballooning behavior and descend, or at least become less active to conserve energy and lower their visibility to predators such as

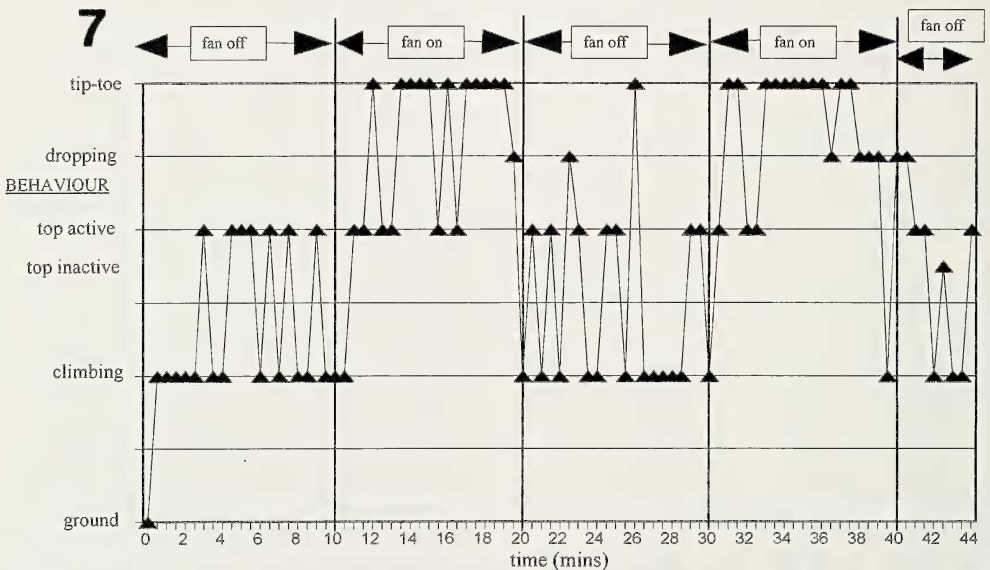


Figure 7.—The effect of air movement on pre-ballooning behavior for spider D. Behavior recorded in 30 second periods with fan on or off.

birds, if ballooning attempts became unsuccessful.

The reason for the FAP type activity observed here is unclear. As mentioned above, spiders normally occupying a niche on or near the ground under dense vegetation must be risking much higher chances of predation by climbing to a prominent position and moving around. It is possible that a FAP to continue the behavior allows for natural changes in the airflow above the vegetation, so the spiders do not continually climb and descend as windspeed rises and falls, thereby possibly missing suitable conditions for take-off attempts.

The temporal shut-off suggested here, in the experiment to determine the duration of ballooning behavior, is not representative of the field, where conditions are not continually suitable or stimulating and there may be enforced breaks in ballooning, as well as the voluntary respites suggested here. Also, in the laboratory flight was not possible, only constant attempts. A period of just 10 minutes of take-off attempts may equate to several successful flights in the field. Thomas (1993) found wide variation in the time between flights in spiders observed ballooning in the field, ranging from 1–66 min, with a modal interval of 1 min before flight was resumed. These times are taken between successful flights and, of course, are subject to changes in conditions for stimulus and flight.

Results here suggest that spiders show highly variable duration of ballooning bouts, interspersed with temporary rest periods which, in combination with variable numbers of flights per day and variable flight distance (Thomas 1993) means that individuals will travel extremely variable distances on a day when conditions are suitable for ballooning. Dispersal will be very high, as will the variety of habitats sampled, compared to a group all travelling the same distance in the same direction and landing more or less in a group downwind from the start point.

It would be extremely useful, in terms of modelling spider spatial dynamics, to observe the full temporal and spatial range of different ballooning behaviors, and distances travelled in flight (and, indeed, cursorily) for a large number of individual spiders in the field. However, it is virtually impossible to follow a spider in flight for more than a short distance, or to follow one through the vegetation. It would also be valuable to discover the full range and nature of the stimuli involved in ballooning in the field, though

expensive equipment and many observation hours are required for accurate meteorological readings to be taken within and above a crop in combination with behavioral observations. Some work of this nature has been undertaken, by Thomas (1993), van Wingerden and Vugts (1974), and by the current author (unpubl.), for example, though the complex interactions between meteorological factors have tended to obscure results pertaining to stimulation of spider ballooning behavior.

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